

## Research papers

# Whitefly wax as a cue for phoresy in the broad mite, *Polyphagotarsonemus latus* (Acari: Tarsonemidae)

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**Summary.** Broad mite, *Polyphagotarsonemus latus* (Acari: Tarsonemidae) exhibits a specific phoretic relationship with whiteflies. Under field conditions most broad mites, caught in sticky traps, are attached to whiteflies. Under laboratory conditions, attachment occurs equally well in the dark and light. Mites do not differentiate between the sexes of their phoretic host *Bemisia tabaci*. However, mite attachment to *B. tabaci* is greatly diminished by washing the host with various organic solvents, chloroform in particular. The effect of whitefly waxy particles on broad mite behavior was studied using wax from the whitefly *Aleyrodes singularis* and from the mealybug *Planococcus citri*. Broad mites were not only attracted specifically to the *A. singularis* waxy particles-treated leaf areas but were also attached to leaf trichomes in this area. The results of this study suggests the importance of olfactory cues from the whitefly waxy particles in the recognition process of the phoretic host and/or the induction of the attachment behavior to whitefly legs or leaf trichomes.

**Key words.** Broad mite – *Polyphagotarsonemus latus* – aldehydes – alcohols – phoresy – chemical cues

## Introduction

Dispersal is an important phenomenon that allows the mite to escape from areas unsuited for further development of the individual or its progeny. Being wingless, Acari are limited in their methods of interplant dispersion to three modes: walking, passive aerial dispersal and phoresy. Walking allows only limited dispersal while the other two methods provide long-distance means of traveling. Phoresy has been described as a phenomenon in which one animal, the phoront, actively seeks out and attaches to an animal of another species, the phoretic host, for dispersal, (Faryish & Axtell 1971). This phenomenon is manifested in all orders of Acari and usually involves insect vectors. Phoretic association may be non-specific, with the phoront potentially using a large range of phoretic hosts, or specific, with

preference towards a family, genus or even a single species (Athias-Binche 1991). Phoresy was extensively studied in Astigmata (Houck & OConnor 1991). Free-living tarsonemid mites (Prostigmata) are fungivores, algivores and herbivores. The latter usually disperse on wind currents. The one known exception to this rule is the broad mite, which is known to have a phoretic association with at least some genera of whiteflies (Homoptera: Aleyrodidae), namely *Bemisia*, *Trialeurodes*, *Aleyrodes* and *Dialeuroides* (Natarajan 1988; Fletchmann *et al.* 1990; Parker & Gerson 1994; Fan & Petit 1998; Palevsky *et al.* 2001). Recently, it was shown that broad mites are able to select between insects of different taxonomic groups. Broad mites preferentially attach to whiteflies whereas other winged insects, that are common on the same host plants, namely thrips and aphids, are rejected (Palevsky *et al.* 2001). These data indicated the existence of a specific recognition of Aleyroids by broad mites. Phoresy can be divided into the following sequential steps: 1) initiation of phoretic behavior by the mite; 2) active host seeking; 3) recognition of attractant signals; and 4) attachment to the host surface. Specific cues may operate at each one of these steps, including attraction from a distance and/or vector recognition during attachment. Recognition of the vector by the mite may involve different cues, visual, tactual and/or chemical. Since broad mite vision is probably limited to light/dark differentiation, visual cues are highly unlikely to play a role in their behavior. However, reflected light from the characteristic white wings of the whiteflies might have some effect on host recognition of broad mites. More likely, vector recognition is probably associated with tactual and chemical cues. Our objectives were to determine the significance of phoresy on whiteflies in mite dispersal and to identify the means of vector recognition by the broad mite.

## Materials and methods

### Field studies of mite dispersal

To assess whether mites entering the screen house were windborne or phoretic on whiteflies, two sets of sticky traps (yellow-attractive to white flies and clear-interference traps only) were set 1 meter above the ground and 1 meter from the wall of a cucumber screen house and positioned windward, facing away from the screen house wall. The traps were composed of a glass microscope slide

coated with a thin layer of water-based adhesive (Rimifoot liquid, Rimi Chemical Co. Ltd., Israel), mounted in a standard Petri dish (9 cm) which was fixed to a yellow or clear plastic board (6 replicates each). Traps were monitored from May through December (total 10 times). Slides were examined under a stereomicroscope for the presence of broad mites and whiteflies (*Bemisia tabaci*). Mites found attached to whiteflies were classified as phoretic while mites found at random were classified as windborne. All mites were placed in warm lactic acid for two hours (serving two purposes, clearing the mites and dissolving remnants of the water based adhesive), mounted in Hoyer's and identified at 400X using a phase contrast microscope.

#### *Broad mite, whitefly rearing and whitefly waxy particles collection*

Standard broad mite culture was established on young potato foliage at the Plant Protection Institute of the Agricultural Research Organization (ARO), Bet Dagan, Israel, as described by Palevsky *et al.* (2001) and maintained at 19–27°C, 30–60% RH. *Bemisia tabaci* were reared on young bean foliage at 25–27°C, 30–60% RH. Both cultures were located at ARO, Bet Dagan. *Aleyrodes singularis* adults and leaves of *Lactuca serriola* coated with *A. singularis* waxy particles were collected in natural areas of the Upper Galilee, Israel, and kept at –20°C, until the experiment was carried out.

#### *Bioassay for phoresy*

Phoresy was assessed by counting the mites attached to frozen insect vectors (24 hrs at –20°C) as described by Palevsky *et al.* (2001), the standard vector being *B. tabaci* females. Vectors were set on detached shoots of potato plants three weeks after infestation. Four hours later, unless specified otherwise, vectors were placed in 96% ethanol and the number of attached broad mites was counted (standard attachment bioassay).

To test the effect of light reflection from whitefly wings on mite attachment, the vector was tested under light and dark conditions. In order to test mite differentiation between the vector's sex we conducted a paired analysis. Two dead whiteflies (one of each sex) were placed 0.15 cm apart on mite infested leaves. Attachment to each whitefly was monitored.

The likelihood of cuticular lipids and/or waxy particles serving as chemical cues in the interaction between broad mites and whiteflies was examined by comparing mite attachment to solvent as well as to untreated *B. tabaci*. Frozen whiteflies were washed for 2 min while agitating in 1.5 ml of either: pentane, dichloromethane, chloroform, ethanol 100%, or ethanol 50% in distilled water. We attempted to restore the attraction of a chloroform prewashed (2 min) *B. tabaci* by reapplication of 0.5 µl of the concentrated chloroform extract (2 whitefly eq/µl).

Considering that among whiteflies the highest attachment levels were found on *A. singularis* (Palevsky *et al.* 2001), and copious amounts of waxy particles of this species are to be found not only on the insect but also on the surrounding leaf surface, we tested the mite attraction to these particles. Three circles (0.5 cm in diameter) were drawn on potato foliage infested with mites. One of the circles was powdered with the waxy particles of *A. singularis*, the second was powdered with waxy particles of the non-host citrus mealybug *Planococcus citri*, and the third circle was left untreated for control. Waxy particles collected from plant material were applied uniformly under a stereo-microscope with a fine paint brush (No 0000). Mite numbers and behavior in each circle were monitored at five intervals (just before waxy particles application and subsequently after 1, 2, 4 and 8 hours).

#### *Chemical analysis of the waxy particles*

The surface lipid samples were obtained from *A. singularis* adults (two replicates of 20 adults each) by placing them in a

chloroform-rinsed champagne funnel plugged with glass wool and then rinsing them with a flow of 6–7 ml of chloroform for 1 min. Waxy particles collected from the leaves of *Lactuca serriola* infested with adults and larvae of *A. singularis* were dissolved in chloroform. The waxy particles of *P. citri* were extracted from the mealybug with chloroform, then the chloroform was evaporated and the waxy particles extracted with *n*-hexane to remove short-chain compounds which were more soluble in hexane than were the long-chain compounds.

Alcohols tend to degrade and chromatograph poorly when analyzed. They can be analyzed as their acetate esters or their trimethylsilyl (TMS) derivatives. We chose to make the TMS derivatives because this procedure also derivatizes free fatty acids enabling the detection of trace amounts of alcohols and fatty acids at the same time. An aliquot of the lipid extract was dried and then derivatized by sequentially adding benzene, BSA (N,O-bis(trimethylsilyl)acetamide and dimethylformamide (2:2:6). The reaction tube was sealed and heated at 76°C for 20 min and then an aliquot was injected (if the volume was too reduced, additional benzene was added.)

The total lipid samples were analyzed by injecting a 1 µl aliquot into a HP (Hewlett Packard = Agilent Technologies, Wilmington, DE, USA) 5890 capillary gas chromatograph with a pressure programmable cool on-column injection port (Nelson *et al.*, 2002) and He carrier gas. The column consisted of a 1-m retention gap connected to a DB-1MS (Agilent Technologies) 12.5-m × 0.2-mm capillary column coupled to a HP 5970B quadrupole mass selective detector. The initial column temperature was 150°C. Five minutes after injection of the sample, data collection and the temperature program were started. The temperature was programmed at 4°C/min to 320°C and held for 20–120 min as necessary for all components to elute. Aldehydes, alcohols, hydrocarbons and wax esters were identified from their mass spectra (Buckner 1993, Nelson 1993, Nelson *et al.* 1994) and the percentage of composition determined (Nelson *et al.* 2000) after adjusting the data for differences in system response to the lipid classes.

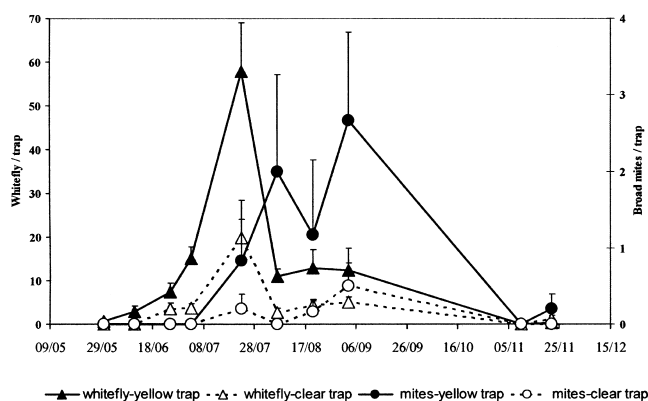
#### *Statistical analysis*

Field studies of mite dispersal were analyzed by Chi-square. Broad mite infestation levels on potato shoots were high (ca. 125 mites/shoot), leading us to assume independence of attachment levels to each of the potential phoretic hosts. To convert attachment levels to continuous data, values were transformed using  $\sqrt{x+0.5}$  (Sokal & Rohlf 1981) and then analyzed by a paired t-test or ANOVA. This was followed by Fisher LSD post-hoc analysis with the Statview package for Power Macintosh, version 4.5, 1992. Time course experiments were analyzed by GLM repeated measures on the transformed data as above (Statgraphics 5 plus for PC, Mangistic INC 2000).

## Results

#### *Field studies of mite dispersal*

The monitoring of broad mites with sticky traps from May through December (Fig 1) indicated that mite dispersal mainly occurred from July to September. The peak trappings for whiteflies and mites were shifted from each other, but in general, periods of major mite trapping coincided with high numbers of *B. tabaci*. Significantly higher trappings of mites were found on yellow traps ( $p < 0.0001$ ,  $X^2$ ). Although the number of mites trapped was low almost all were phoretic: 92.3% of 36 mites found on yellow traps and all 5 mites found on the clear traps. Less than 2% of the *B. tabaci* ( $n = 922$ ) trapped carried broad mites.



**Fig. 1** Broad mite and *Bemisia tabaci* trapped on clear vs. yellow traps (data are means plus SEM,  $n = 6$ )

#### *The role of optical cues play a role in phoretic host recognition by mites*

Lighting conditions did not seem to affect mite-vector recognition abilities, as similar attachment levels of 4–5 mites per whitefly took place both under dark ( $5.5 \pm 1.09$ ) and light ( $4.7 \pm 1.6$ ) conditions. The attachment levels were even a little higher under dark conditions but these differences were not significant.

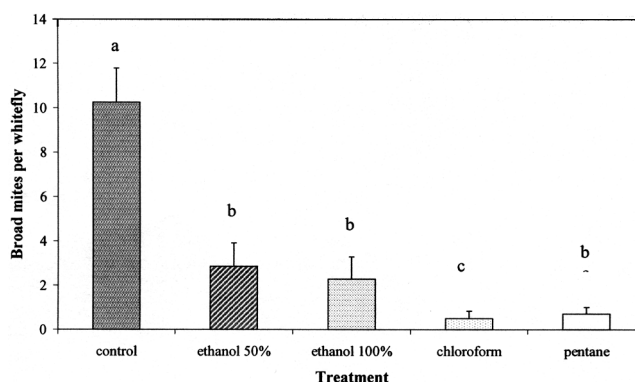
#### *Does sex of the host play a role in phoretic host recognition by mites?*

Some sex specific differences in size and shape are visible in *B. tabaci*. Although attachment to females seems to be preferred, no significant difference in attachment to males ( $11.0 \pm 2.06$ ) and females ( $15.2 \pm 2.7$ ) was detected (paired t-test,  $p = 0.165$ ).

#### *The impact of chemical cues on attraction to and/or recognition of insect vectors*

Mite attachment to the standard phoretic host (*B. tabaci*) was diminished by washing the host with various solvents (Fig 2) (ANOVA,  $p < 0.0001$ ). In general, attraction to the host was inversely related to the polarity of the washing solution. The most effective solvent was chloroform. However, application of the concentrated chloroform extract failed to restore mite attraction to the chloroform washed *B. tabaci*, since no mites attached to extract treated whiteflies.

Waxy particles of *A. singularis* but not of *P. citri* caused a significant attraction of mites to wax treated patches, within an hour of the application ( $12 \pm 2.1$  mites/circle, Fig 3A,  $p < 0.01$ , GLM, repeated measures). Although this attraction subsequently became weaker, it stood firm for up to at least 8 hours. Moreover, we observed attachment of broad mites to trichomes on leaves treated with waxy particles of *A. singularis* (Fig 4). The mode of attachment to trichomes was similar to that observed to the legs of their phoretic hosts. Trichome attachment peaked one hour after



**Fig. 2** The effect of washing of *Bemisia tabaci* on mite attachment (Data are means plus SEM, of at least 8 replicates). Columns with different letters are significantly different (ANOVA, followed by Fisher PLSD on transformed data,  $p < 0.05$ )

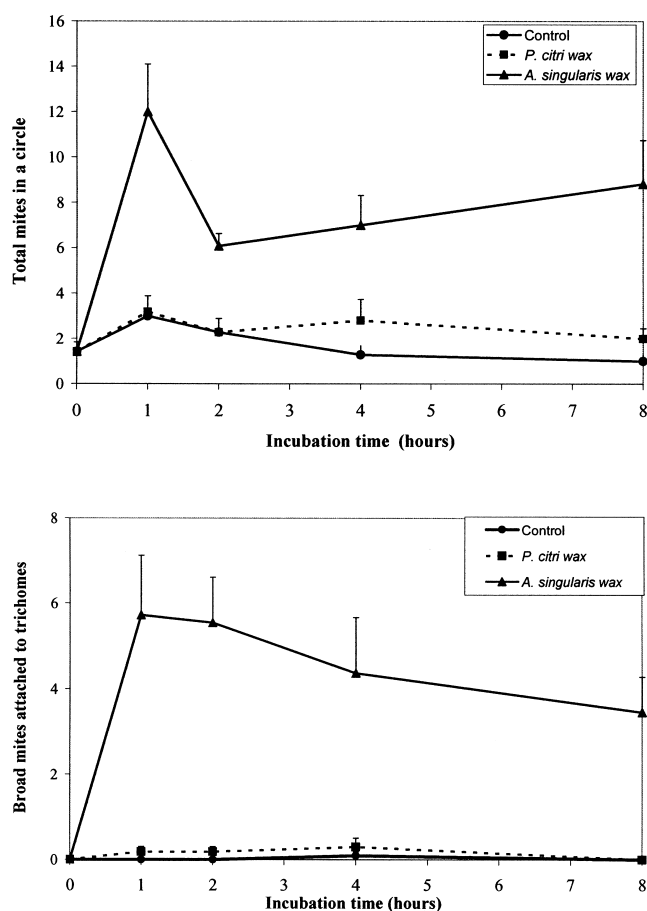
application at a mean of  $5.7 \pm 1.4$  attached-mites/circle and decreased thereafter, though remaining significant even after 8 hours (Fig 3B,  $p < 0.001$ , GLM, repeated measures).

#### *Chemical analysis*

Chemical analysis of the external lipids of adult *A. singularis* and wax particles of *A. singularis* deposited on its host plant revealed about 106 components. The composition of 30 main components is presented in Table 1. Despite some variation between the samples, about 70% congruency can be detected between the composition of lipids from adults and wax particles collected from leaves. Although four groups of compounds could be detected, the dominant components were long-chain aldehydes and alcohols, the most prominent being a 32-carbon aldehyde (dotriacontanal) and a 32-carbon alcohol (dotriacontan-1-ol). On the other hand, *P. citri* waxy particles did not contain any aldehydes or long chain alcohols and only trace amounts of alcohols were identified after treatment of the sample with BSA (Data not shown).

## Discussion

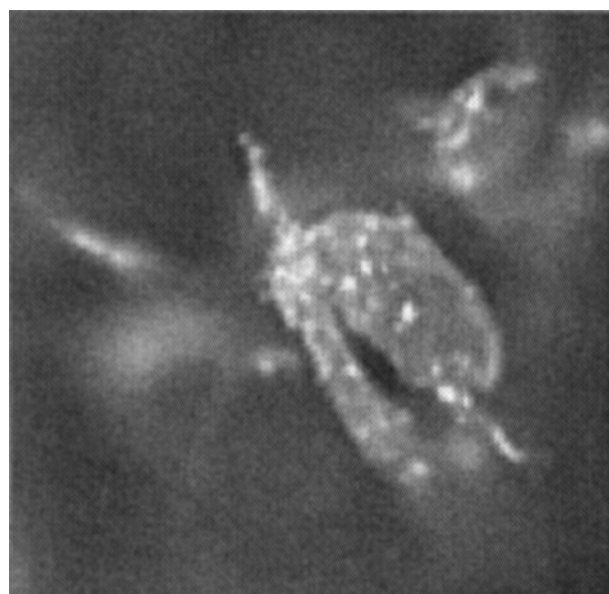
The phoretic association between broad mite and polyphagous insects living on the same plants constitutes for *P. latus* an efficient mode of dispersal from one host patch to another. Our data indicate that passive wind dispersal is very limited. Although broad mite-whitefly phoretic association appears to be facultative, the monitoring of broad mites with sticky traps near greenhouses clearly indicates the importance of phoresy in broad mite dispersal and epidemiology. The low number of whiteflies carrying mites could result from a number of reasons: mites found on a few plants visited by whiteflies, whiteflies do not remain stationary long enough for mites to attach or they even resist such attachments. The importance of phoresy becomes apparent despite these low numbers when taking into account that in broad mite only mature and most likely mated females are phoretic (Palevsky *et al.* 2001) and the fact that this mite has an extremely short life cycle (just 5–6 days at 25°C, Gerson 1992).



**Fig. 3** Time course of the effect of *Aleyrodes singularis* and *Planococcus citri* waxes vs control on broad mite behavior: A. Mites within patch. B. Broad mite attachment to leaf trichomes within patch (means plus SEM, of at least 10 replicates)

In terms of broad mites, the association with whiteflies is specific (Palevsky *et al.* 2001). But what are the specific cues involved in recognition of the whiteflies by broad mites and at what stages of phoresy do they operate? By showing that attachment to the phoretic host occurs equally well under dark and light conditions we eliminated the possibility of involvement of any visual cues in the recognition process. Although some physical differences exist between males and females of *B. tabaci*, broad mites did not differentiate between the sexes of the host. This may not be surprising since both sexes disperse long distances and may act as a good vector even though they differ in both behavior and life span (Blackmer & Byrne 1993). Attaching to males that fly longer and cover larger distances, or to females that live longer, apparently provides similar chances to reach a suitable feeding source thereby eliminating selective pressure for discrimination between the sexes.

Olfaction is probably the main mechanism operating in host recognition. Reduction of attachment to the host, following its brief solvent washing could be caused by the application of the solvent, the removal of surface lipids, or both. The lowest attachment following the chloroform wash



**Fig. 4** Attachment of broad mite to trichome on leaf treated with waxy particles of *A. singularis*

further suggests the waxy nature of the recognition cues, removal of which disrupted the host recognition by broad mites. Failure to restore attractivity of whiteflies to broad mites by the application of chloroform extracts could be due to residual chloroform that remained within the body of treated whiteflies (Nelson, unpublished data), possibly acting as a repellent to the broad mites.

The external lipids of adult whitefly could be differentiated into two categories: the waxy particles and the lipids of the cuticular surface. The waxy particles consist mainly of long chain alcohols and aldehydes. The cuticular surface lipids of adults are wax esters and minor amounts of hydrocarbons, largely *n*-alkanes (Nelson *et al.* 1994, 1997, 1998). No sex specific differences in wax ester composition were detected between the biotypes A and B of *Bemisia tabaci* (Nelson *et al.* 1994). Chemical composition of lipids found in *A. singularis* waxy particles collected from the leaves were similar to those observed from the adults. There are some differences in the composition of external lipids between those of the adults and those collected from the leaves. These could have originated from nymphs and/or their exuvia.

We hypothesize that attractants are present in the waxy particles of the broad mite phoretic host and the lack of these attractants will affect host location and attraction. This hypothesis is supported by the observations that broad mites are attracted specifically to leaf surfaces treated with crude waxy particles from the whitefly *A. singularis* but not to the waxy particles obtained from the non-host *P. citri*. Indeed, differences in chemical composition of the waxy particles are found between the non-host *P. citri* and the *A. singularis*. These are particularly expressed by the absence of aldehydes and long chain alcohols in *P. citri*. As mentioned previously, these compounds are characteristic to all whiteflies evaluated so far that do attract broad mites.

**Table 1** The main components of the external lipids of adult *Aleyrodes singularis* and their waxy particles deposited on its host plant *Lactuca serriola*. Components were identified from their mass spectra. Fatty acids and alcohols were identified as their TMS ester and ether derivatives, respectively. Results are presented as percent of total. Only peaks that constituted more than 1% of the total lipids identified by GC-MS are presented

Substances	Adults Sample #1	Adults Sample # 2	Wax particle Sample #1	Wax particle Sample #2
<b>Free fatty acids</b>				
Hexadecanoic	1.2	3.3	1.2	0.5
Octadecadienoic	0.8	5.6	0.6	0.3
Octadecenoic	1.1	6.9	0.8	0.3
Octadecanoic	2.0	4.6	2.1	0.8
Hentriacontanoic	0.0	1.1	0.5	0.3
Dotriacontanoi	0.8	1.9	1.6	0.4
<b>Alcohols</b>				
Hexacosanol	0.1	0.1	1.3	1.6
Dotriacontanol	4.4	13.6	8.3	4.1
<b>Aldehydes</b>				
Hexacosanal	0.0	0.0	1.5	0.7
Triaccontanal	8.8	4.6	2.3	2.1
Dotriacontanal	46.1	27.0	31.0	60.8
Trtriacontanal	0.0	0.0	1.4	1.0
Tetratriacontanal	4.3	2.8	3.0	6.9
<b>Alkanes</b>				
Heptacosane	0.9	0.7	1.2	0.4
Octacosanal	0.7	0.6	2.2	0.9
Hentriacontane	0.6	0.3	1.3	1.4
Dotriacontane	0.6	0.3	1.4	1.0
Tetratriacontane	0.0	0.4	1.4	1.1
Pentatriacontane	0.0	0.0	0.0	2.0
Hexatriacontane	0.7	0.4	1.0	1.2
Heptatriacontane	0.0	0.0	1.1	0.5
<b>Wax esters*</b>				
Docosanoyl hexadecanoate	1.2	1.1	0.5	0.0
Octadecanoyl icosanoate <sup>1</sup>				
Docosanoyl octadecanoate	1.2	1.0	0.9	0.7
Tetracosanoyl hexadecanoate <sup>1</sup>				
Docosanoyl icosanoate				
Tetracosanoyl octadecanoate <sup>1</sup>				
Hexacosanoyl hexadecanoate <sup>1</sup>	2.8	3.1	2.2	0.3
Docosanoyl docosanoate				
Hexacosanoyl octadecanoate <sup>1</sup>				
Tetracosanoyl icosanoate <sup>1</sup>				
Octacosanoyl hexadecanoate <sup>1</sup>				
Icosanoyl tetracosanoate <sup>1</sup>	2.5	2.6	1.6	0.0
Docosanoyl tetracosanoate <sup>a</sup>				
Tetracosanoyl docosanoate				
Hexacosanoyl icosanoate <sup>1</sup>				
Octacosanoyl octadecanoate <sup>1</sup>				
Triaccontanoyl hexadecanoate <sup>1</sup>	0.9	0.9	1.2	0.0
Dotriacontanoyl hexadecanoate <sup>1</sup>				
Triaccontanoyl octadecanoate <sup>1</sup>				
Tetracosanoyl tetracosanoate	0.6	0.5	1.7	0.8
Dotriaconanoyl octadecanoate <sup>a</sup>				
Hexacosanoyl tetradecanoate <sup>1</sup>	0.5	0.5	6.2	1.4
Unknown				
?	1.6	1.0	0.0	0.0
?	1.5	0.8	0.0	0.0

\*In some cases appeared to be mixtures of <sup>a</sup>isomers that appear only in adults, <sup>1</sup>isomers that appear only in wax particles collected on leaves listed in decreasing order on abundance.

The fact that broad mites were not only attracted to the waxy particles but were even attached to leaf trichomes treated with the *A. singularis* waxy particles is fascinating. This attachment similar in manner observed to the legs and antennae of their phoretic host further suggests the involvement of whitefly waxy particles not only in the recognition process of the phoretic host but also in the inducement of the attachment behavior. The composition of the attractants remain to be identified.

## Acknowledgments

We wish to thank Dr. Issac Ishaaya and Svetlana Kontsedalov (both Volcani Center, ARO) for providing the *Bemisia tabaci* used in our attraction studies, Fausi AbuMoach (Neve Yaar, ARO) for his assistance in monitoring broad mite dispersal and to Dr. Anat Zada (Volcani Center, ARO) for preparation of *P. citri* waxy particle extractions. This manuscript is contribution no. 505/03 of the Institute of Plant Protection, Volcani Center, ARO, Israel.

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Received 22 April 2003; accepted 12 June 2003.



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